Cuticular Hydrocarbons of *Kapala sulcifacies* (Hymenoptera: Eucharitidae) and Its Host, the Ponerine Ant *Ectatomma ruidum* (Hymenoptera: Formicidae)

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ABSTRACT   Cuticular hydrocarbons from the ponerine ant *Ectatomma ruidum* Roger and a highly integrated eucharitid myrmecophile, *Kapala sulcifacies* (Cameron), associated with it, have been characterized. Ninety hydrocarbons were identified from the ant, 55 hydrocarbons from the female wasp and 54 hydrocarbons from the male wasp. The wasps and ants share 40 hydrocarbons. These shared 40 hydrocarbons represent 92.6% of their hydrocarbon composition for female *Kapala*, 84.3% for male *Kapala* and 67.7% for the ants. The wasps have a carbon number range of C_{27} to C_{35}; the ants have a range of C_{23} to C_{35}. Both species possess n-alkanes, C_{27} to C_{33} for the wasps, C_{23} to C_{34} for the ants. Both species also possess major quantities of Z-7- and Z-9 alkenes: C_{29} to C_{33} for the wasps; C_{23} to C_{35} for the ants. The female wasps possess a low amount of a conjugated C_{31} diene (neither the ants nor the male wasps possess this hydrocarbon), and the ants, but not the wasps, contain low quantities of nonconjugated dienes (carbon numbers of C_{23} to C_{29}) with double bonds at Δ^9, and Δ^{14}. Both wasps and ants share homologous series of 3-, 5-, 10-, 11-, 12-, 13-, 15- and 17-methyl branched alkanes. Ants and wasps also share a homologous series of 3,7-dimethyl alkanes. Other internally branched dimethyl alkanes are found in both ants and wasps, but only 11, 15-$DiMeC_{29}$ is shared. Wasps have 7, 15- and 10, 14-dimethyl alkanes while the ants have 15,19-dimethyl alkanes. *Kapala sulcifacies* and *E. ruidum* both possess hydrocarbons of the 5, X-, 11, X-, 12, X- and 13, X-DiMe series, but the compounds involved are not shared because they represent different compounds. Behavioral observations indicate that the ants accept the newly emerged adult parasitoids with no evidence of agonistic behavior for a period of time after adult eclosion. Nevertheless, the chemical deception is not completely efficient because young adult *Kapala* are soon ejected from the nest by transportation by their host. These transportations frequently occur after seizure at the base of the wasps' characteristic scutellar spines, such structures allowing for easy transportation without injury for the parasite. Moreover, if no method of escaping the colony is provided, the ants ultimately attack the parasitoids. The substantial chemical overlap of the cuticular hydrocarbon profiles of the ants and wasps are discussed in the context of the social life of the colony.

KEY WORDS   *Kapala sulcifacies, Ectatomma ruidum,* species recognition, parasite, mass spectrometry, semiochemicals

MOST SOCIAL INSECTS maintain a closed society that excludes all but their own conspecific colony members (Wilson 1971). Cuticular hydrocarbons have been postulated as the primary chemical cue involved in species and kin recognition systems (Howard and Blomquist 1982, Bonavita-Cougourdan et al. 1987). However, numerous inquilines and parasitoids have succeeded in integrating themselves into the life of the colony (Kistner 1979). The mechanisms by which they achieve this integration are known for a variety of inquilines and predators and for one species of parasitoid (Howard and Blomquist 1982; Howard et al. 1990a, 1990b; Vander Meer et al. 1989; Lenoir et al. 1997). Here again, cuticular hydrocarbons are impli-

cated, and they have been hypothesized to function in chemical camouflage or chemical mimicry (Vander Meer and Wojcik 1982; Vander Meer et al. 1989; Howard et al. 1990a, 1990b; Dettner and Liepert 1994), depending on whether the cuticular hydrocarbons of the host were acquired by contact or by de novo biosynthesis by the inquiline/parasite.

All eucharitids of the subfamily Eucharitinae (Hymenoptera, Eucharitidae) are specific parasitoids of ants (Heraty and Darling 1994, Heraty 1994a). Females deposit their eggs in or on plant tissue where the ant host is likely to forage. It is the first-instar larva, the planidium (active, specialized, sclerotized larva) that faces the problem of host recognition and attachment to the correct ant species before being passively transported to the host nest by phoresis. Within the ant nest, it moves to a larva and continues its development only when the host larva begins to pupate (Clausen 1941, Johnson et al. 1986, Heraty 1994b).

The genus *Kapala* Cameron is the most frequently collected of the seven genera of Eucharitinae known

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in Central America (Heraty 1995), although only a few of its species can be accurately identified (Heraty and Wooley 1993). Nevertheless, information dealing with its biology and behavior remain very scarce, and detailed knowledge of the nature of its relationships with its hosts is unknown. For a long time, the only hosts of *Kapala* reported in the literature referred to large ponerine ant species of the genera *Pachycondyla* and *Odontomachus* (Myers 1931; Clausen 1940, 1941). Recently, two other ponerine genera of middle size, *Ectatomma* (Lachaud et al. 1998a) and *Gnamptogenys* (Lachaud et al. 1998b, Lachaud and Pérez-Lachaud 2001), have been reported as new hosts for *Kapala*, making the range of potential hosts for this parasitoid genus the largest known among Eucharitinae. Among Eucharitidae, such a comparable range of potential host genera has only been reported within the Oraseminae subfamily for the genus *Orasema*, which is also known to attack four ant genera: *Solenopsis*, *Pheidole*, *Wasmannia*, and *Formica* (Johnson et al. 1986; Heraty 1994a, 1994b).

Adults of *K. sulcifacies* (Cameron) were first observed in February 1995 (J.P.L., unpublished data) while looking at various colonies of the neotropical ponerine ant *Ectatomma ruidum* Roger, collected at "Finca San-Antonio," a cocoa plantation, in Izapa, near Tapachula (Chiapas, Mexico). Since that date, adult males and females have been repeatedly encountered in association with this ant species at various sites in the same region. Direct observations on the interaction between adult *K. sulcifacies* and its host *E. ruidum* showed that worker ants did not exhibit agonistic behavior toward newly emerged adult wasps, leading us to hypothesize that the cuticular hydrocarbon profile of *K. sulcifacies* adults may resemble that of their host as previously shown for *Orasema xanthopus* (Cameron) and its host *Solenopsis invicta* Buren (Vander Meer et al. 1989). In this article, we give a brief account of the behavioral interactions between the parasitoid wasp and its host and describe cuticular hydrocarbon profiles and possible semiochemical functions of these hydrocarbons.

Materials and Methods

Insects. In Central and South America, the ground-nesting ponerine ant *E. ruidum* is a dominant species in various ecosystems ranging from forest zones (Kugler and Hincapié 1983) to cultivated areas of economic importance, such as cocoa, coffee and maize plantations (Lachaud 1990, Perfecto 1991). Colony size was estimated at ≈90 workers (range, 20–330 workers) (Lachaud et al. 1996), but due to both the very high nest densities (up to 11,000 nests/ha, Schatz et al. 1998) and its important predatory impact on insect pests, this species has been considered a valuable natural agent of biological control in various agro-ecosystems (Weber 1946, Perfecto 1991, Lachaud et al. 1996).

During the first 2 wk of July 1998, 59 nests of *E. ruidum* were completely excavated from two sites located in a cocoa plantation (Rancho San Antonio) at Izapa, Tuxtla Chico, Chiapas, Mexico (400 m above sea level, 15 km NE of Tapachula) and 5 km further along the road from the previous site in a coffee plantation of the Experimental Station INIFAP at Rosario Izapa, Tuxtla Chico (430 m above sea level, 18 km E-NE of Tapachula). For each colony, the cocoons were separated in a glass tube and checked twice a day to collect adult *K. sulcifacies* males and females at emergence from host cocoons. After four days of such a survey, the number and stage of development of parasitoids present in the nests were determined by dissecting all the remaining cocoons and carefully looking for developmental stages (including planidia attached to host prepupae) under a stereomicroscope (40×).

In addition, observations were made in the laboratory on two parasitized queenright colonies of *E. ruidum* (from a previous collection) to video-tape the interaction between the parasitoid wasps and their hosts at the moment of eclosion. Due to the presence of two elongate cylindrical spines at the apex of the parasitoid scutellum, ant cocoons containing mature *K. sulcifacies* pupae nearly ready to eclose can be easily recognized by examination under transmitted light. The eclosion of two adult wasps from such cocoons was recorded.

Sample Preparation and Extraction. Adult *K. sulcifacies* males and females collected at emergence from host cocoons were placed individually or in groups of five individuals in 7-ml glass vials that contained 1 ml HPLC-grade n-hexane (Merck, West Germany) and slightly shaken for 1 min. The hexane was transferred by Pasteur pipet to 8-ml vials, and the procedure repeated two more times. The combined portions from each replicate were concentrated under a gentle stream of N_2 to almost dryness. Samples were shipped by mail to the Grain Marketing and Production Research Center, Manhattan, KS, and reconstituted with pesticide-grade hexane before analysis by gas chromatography-mass spectrometry. Worker ants originating from the same colonies as adults eucharitids were also extracted using the same procedure. A sample of host ants and parasitoids were preserved in 70% ethanol, and voucher specimens were deposited in the entomological collection of El Colegio de la Frontera Sur (San Cristobal de las Casas, Chiapas) and at the University of California, Riverside.

Hydrocarbon Analysis. Each sample was concentrated under a stream of N_2, and hydrocarbons were isolated by chromatography on a 3 cm "mini-column" of Biosil A (Bio-Rad, Richmond, CA) as described earlier (Howard et al. 1978). Electron impact mass spectral analyses were conducted using a Hewlett–Packard 5790A gas chromatograph (GC) (Hewlett–Packard, San Fernando, CA) containing a DB-5 bonded phase capillary column (15 m long, 0.25 mm i.d.) (J & W Scientific, Folsom, CA) connected to a Hewlett–Packard 5970 mass selective detector (MSD) and a Hewlett–Packard 9133 data system. Ultrapure helium was the carrier gas, with a column head pressure of 0.75 kg/cm^2. Mass spectra were obtained at 70 eV. Analyses were done using temperature programming, with an initial temperature of

80°C, a final temperature of 320°C, a program rate of 5°C/min, and a 20-min final hold period. The splitless injector was set at 275°C, and the GC/MSD interface was set at 280°C. Retention times of each hydrocarbon component and equivalent chain length values (ECL) were obtained by comparison with known *n*-alkane standards (Howard et al. 1978). Individual components in the total ion scanning mode were identified from their characteristic EI-MS fragmentation patterns (Jackson and Blomquist 1976, Nelson 1978). Quantitative analyses were conducted using the total ion scanning mode.

Double-bond locations in alkenes were obtained by preparing dithiomethyl ethers and examining their electron impact mass spectra (EI-MS) (Francis and Veland 1981). Stereochemistry of the parent alkene was established from comparison of retention times of dithiomethyl ethers of insect-derived olefins to dithiomethyl ethers of known olefin stereoisomers. A DB-5 bonded phase capillary column (15 m long, 0.25 mm i.d.) using chromatographic conditions identical to those described above was used.

Results

Host Ant Workers–Adult Parasitoids Interactions. Out of the 59 colonies of *E. ruidum* collected, 51 (86.4%) were parasitized by one or more parasitoids (3.6 ± 3.2 eucharitids per parasitized nest; range: 1–16). A total of 182 *K. sulcifacies* was obtained: 18 adult females, 18 adult males, eight damaged adults, 24 female pupae, 44 male pupae, three damaged pupae, and 67 developmental stages (planidia, second and third instar larvae, prepupae). For the studied population and the period concerned (July), the parasitism impact (based on the ratio between the number of juvenile stages + adult parasitoids and the number of host pupae) was 7.3 ± 5.9%.

Analysis of two video-taped eucharitid eclosion sequences indicated that no apparent distinction could be made in the behavior of the host workers faced with parasitized and unparasitized cocoons, which are grouped together in the same chambers. Both are frequently antennated and quickly removed at any disturbance. At the moment of eclosion, workers are very active around the cocoons. They assist the hatching wasps, tearing the silk and drawing forth the young adults, which extricate from the envelope and immediately spread out and dry their wings. In the same manner as with callow nestmates, workers of *E. ruidum* exhibit considerable interest (antennation, grooming) toward the young parasites, which, most of the time, freeze at the host contact. Soon after eclosion, the young adult wasps actively endeavor to leave the nest and can attain the exit by their own means. In most cases, however, they are assisted by their host, in a similar way to that described for *E. tuberculatum* (Olivier) and its associated eucharitid parasitoid (Lachaud et al. 1998c): after seizure by a worker without any aggressive behavior, they are transported within the nest for a short distance before being released. The transport posture does not correspond to the typical folded position over the head normally

used in adult transport by *E. ruidum* (Möglich and Hölldobler 1974, Pratt 1989): regularly, but not exclusively, the eucharitids are seized at the base of their scutellar spines and held forward of the worker's head, like a "wheelbarrow." During such transportation, the eucharitids remain quiescent. Progressively, the transportation by the host workers become increasingly frequent, the distance carried becomes greater and the ants orient more precisely to the nest exit until the parasites are finally ejected outside the nest. Several different host workers are often involved at different times in such ejection behavior, with a break between bouts. If the ejection occurs in an experimental container with no lid, the parasites fly away at once. If they are experimentally reintroduced within the colony, the host workers rapidly renew the passive transportation to the nest exit, but after a few repetitions, the successive contacts with ant workers become more and more aggressive (mandible opening, bite, gaster flexion with sting extrusion). In the laboratory, without the real possibility of going out of the artificial colony, the eucharitids are killed within 2–3 d after eclosion and immediately dismembered. The host ants were never observed feeding the adult wasps.

Cuticular Hydrocarbons of Ants and Parasitoids. The hydrocarbon composition of *E. ruidum*, like most ants (Howard et al. 1990a, Kaib et al. 1993, Bonavita-Cougourdan et al. 1996, Lenoir et al. 1997, Monin et al. 1998, Liebig et al. 2000, Trabalon et al. 2000), is complex, containing normal and branched alkanes, as well as alkenes and alkadienes (Tables 1 and 2). n-Alkanes of carbon number 23–34 comprise ≈21% of the hydrocarbons. An additional ≈42% of the ant hydrocarbons are composed of branched alkanes. Monomethyl alkanes (35%) include homologous series of 3-, 5-, 9-, 10-, 11-, 12-, 13-, 15- and 17-methyl alkanes. Dimethyl alkanes (7%) are homologous series of 3, 7-, 5, 11-, 5, 13-, 11, 19-, and 13, 17-dimethyl alkanes, and a series of dimethyl alkanes with branching patterns of 5,9-, 11,15-, 11, 20-, 11, 21-, 12, 21-, 13,19- and 15,19-. The remaining ≈37% of hydrocarbons on *E. ruidum* are mono- and dienes. The monoenes (34%) are isomeric mixtures of Z-7- and Z-9- compounds with carbon numbers between 23 and 35. The Z-9- isomers are always present in greater abundance than the Z-7-isomers. Ant dienes (3%) have carbon numbers from 23 to 29 with compounds being Z,Z-9,14-isomers. No conjugated dienes were found.

The cuticular hydrocarbon composition of the newly emerged male and female parasitoids is very similar to that of the host ants (Tables 1 and 3). Some differences do occur, however, and distinct gender based differences are found between the wasp sexes. The n-alkanes of the wasps have a carbon number range of 27–33 and constitute ≈19% of the female hydrocarbons and 26% of the male hydrocarbons (Table 4). Branched alkanes make up ≈50% of the female hydrocarbons and ≈65% of the male hydrocarbons. Monomethyl alkanes (43% of the female hydrocarbons and 49% of the male hydrocarbons) are homologous series of 3-, 4-, 5-, 11-, 12-, 13-, and 15-methyl alkanes, and a series of methyl alkanes with

Table 1. Cuticular hydrocarbons of *Ectatomma ruidum* (Er) and *Kapala sulcifacies* (Ks)

Compound	CN^a	ECL^b	Er	Ks	Diagnostic mass spectral ion fragments $(m/z)^{c,d}$
9,14-$C_{23:2}$	23	22.66	+	−	320 (61, 173, 446)
Z-9-$C_{23:1}$	23	22.73	+	−	322 (61, 173, 241, 416)
C_{23}	23	23.00	+	−	324
9-Me C_{23}	24	23.35	+	−	141, 225, 323 (M-15)
9,14-$C_{25:2}$	25	24.67	+	−	348 (61, 173, 201, 474)
Z-9-$C_{25:1}$	25	24.72	+	−	350 (173, 271, 444)
Z-7-$C_{25:1}$	25	24.79	+	−	350 (145, 299, 444)
C_{25}	25	25.00	+	−	352
9-Me C_{25}	26	25.36	+	−	141, 253, 351 (M-15)
11-Me C_{25}	26	25.36	+	−	169, 225, 351 (M-15)
13-Me C_{25}	26	25.36	+	−	197, 351 (M-15)
5-Me C_{25}	26	25.50	+	−	85, 309, 351 (M-15)
3-Me C_{25}	26	25.75	+	−	337, 309
5,11-DiMe C_{25}	27	25.82	+	−	85, 323, 183, 225, 365 (M-15)
5,13-DiMe C_{25}	27	25.82	+	−	85, 197, 211, 365 (M-15)
C_{26}	26	26.00	+	−	366
3,7-DiMe C_{25}	27	26.05	+	−	127, 351, 365 (M-15)
10-Me C_{26}	27	26.35	+	−	155, 253, 365 (M-15)
12-Me C_{26}	27	26.35	+	−	183, 225, 365 (M-15)
9,14-$C_{27:2}$	27	26.66	+	−	376 (61, 173, 229, 502)
Z-9-$C_{27:1}$	27	26.72	+	−	378 (173, 299, 472)
Z-7-$C_{27:1}$	27	26.79	+	−	378 (145, 327, 472)
C_{27}	27	27.00	+	+	380
9-Me C_{27}	28	27.35	−	+	141, 281, 379 (M-15)
11-Me C_{27}	28	27.35	+	+	169, 253, 379 (M-15)
13-Me C_{27}	28	27.35	+	+	197, 225, 379 (M-15)
7-Me C_{27}	28	27.38	−	+	113, 309, 379 (M-15)
5-Me C_{27}	28	27.51	+	+	85, 337, 379 (M-15)
11,19-DiMe C_{27}	29	27.66	+	−	169, 267, 141, 295, 393 (M-15)
3-Me C_{27}	28	27.75	+	+	337, 365, 379 (M-15)
5,11-DiMe C_{27}	29	27.83	+	−	85, 351, 183, 253, 393 (M-15)
5,13-DiMe C_{27}	29	27.83	+	−	85, 351, 211, 225, 393 (M-15)
C_{28}	28	28.00	+	+	394
3,7-DiMe C_{27}	29	28.05	+	+	379, 127, 309, 393 (M-15)
10-Me C_{28}	29	28.35	+	+	155, 281, 393 (M-15)
11-Me C_{28}	29	28.35	−	+	169, 267, 393 (M-15)
12-Me C_{28}	29	28.35	+	+	183, 253, 393 (M-15)
4-Me C_{28}	29	28.55	−	+	71, 365, 393 (M-15)
10,14-DiMe C_{28}	30	28.58	−	+	155, 295, 225, 407 (M-15, not observed)
9,14-$C_{29:2}$	29	28.67	+	−	404 (61, 173, 257, 530)
Z-9-$C_{29:1}$	29	28.72	+	+	406 (173, 327, 500)
3-Me C_{28}	29	28.75	+	+	379, 365, 393 (M-15)
Z-7-$C_{29:1}$	29	28.79	+	+	406 (145, 355, 500)
C_{29}	29	29.00	+	+	408
9-Me C_{29}	30	29.35	+	−	141, 309, 407 (M-15)?
11-Me C_{29}	30	29.35	+	+	169, 281, 407 (M-15)
13-Me C_{29}	30	29.35	+	+	197, 253, 407 (M-15)
15-Me C_{29}	30	29.35	−	+	225, 407 (M-15)
5-Me C_{29}	30	29.51	+	+	85, 365, 407 (M-15)
11,15-DiMe C_{29}	31	29.55	+	+	169, 295, 225, 239, 421 (M-15)
13,17-DiMe C_{29}	31	29.55	+	−	169, 295, 239, 225, 421 (M-15)
11,19-DiMe C_{29}	31	29.64	+	−	169, 295, 421 (M-15)
3-Me C_{29}	30	29.75	Er	+	393, 365, 407 (M-15)
5,9-DiMe C_{29}	31	29.77	+	−	85, 155, 309, 379, 421 (M-15)
C_{30}	30	30.00	+	+	422
3,7-DiMe C_{29}	31	30.05	+	+	407, 127, 337, 421 (M-15)
12-Me C_{30}	31	30.35	+	−	183, 281, 421 (M-15)
4-Me C_{30}	31	30.55	−	+	393, 421 (M-15)
10,14-DiMe C_{30}	32	30.58	−	+	155, 323, 225, 253, 435 (M-15)
11,20-DiMe C_{30}	32	30.62	+	−	169, 309, 435 (M-15)
$C_{31:2}$	31	30.62	+	−	432
Z-9-$C_{31:1}$	31	30.72	+	+	434 (173, 355, 528)
Z-7-$C_{31:1}$	31	30.79	+	+	434 (145, 383, 528)
C_{31}	31	31.00	+	+	436
$C_{31:2}$ (conjugated)	31	31.15	−	+	432
9-Me C_{31}	32	31.35	+	−	141, 337, 435 (M-15)
11-Me C_{31}	32	31.35	+	+	169, 309, 435 (M-15)
13-Me C_{31}	32	31.35	+	+	197, 281, 435 (M-15)
15-Me C_{31}	32	31.35	+	−	225, 253, 435 (M-15)
5-Me C_{31}	33	31.52	+	−	85, 393, 435 (M-15)
11,19-DiMe C_{31}	33	31.60	+	−	169, 323, 197, 295, 449 (M-15)
11,15-DiMe C_{31}	33	31.60	−	+	169, 323, 239, 253, 449, 464
3-Me C_{31}	32	31.72	+	+	421, 393, 435 (M-15)

Table 1. Continued

Compound	CN[a]	ECL[b]	Er	Ks	Diagnostic mass spectral ion fragments $(m/z)^{c,d}$
5,11-DiMe C_{31}	33	31.86	+	−	85, 407, 183, 309, 449 (M-15)
5,13-DiMe C_{31}	33	31.86	+	−	85, 407, 211, 281, 449 (M-15)
C_{32}	32	32.00	+	+	450
3,7-DiMe C_{31}	33	32.05	+	+	435, 127, 365, 449 (M-15)
12-Me C_{32}	33	32.28	+	+	183, 309, 449 (M-15)
12,21-DiMe C_{32}	34	32.57	+	−	183, 323, 463 (M-15)
12,16-DiMe C_{32}	34	32.58	−	+	183, 323, 253, 463 (M-15, not observed)
Z-9-$C_{33:1}$	33	32.72	+	+	462 (173, 383, 556)
Z-7-$C_{33:1}$	33	32.79	+	+	462 (145, 411, 556)
C_{33}	33	33.00	+	+	464
11-Me C_{33}	34	33.35	+	+	169, 337, 463 (M-15)
13-Me C_{33}	34	33.35	+	+	197, 309, 463 (M-15)
15-Me C_{33}	34	33.35	+	+	225, 281, 463 (M-15)
11,21-DiMe C_{33}	35	33.56	+	−	169, 351, 197, 323, 463 (M-15)
13,19-DiMe C_{33}	35	33.56	+	−	197, 323, 225, 295, 463 (M-15)
11,15-DiMe C_{33}	35	33.60	−	+	169, 351, 239, 281, 463 (M-15)
13,17-DiMe C_{33}	35	33.60	−	+	197, 323, 253, 267, 463 (M-15)
7,15-DiMe C_{33}	35	33.68	−	+	127, 407, 239, 281; 477 (M-15)
5,15-DiMe C_{33}	35	33.72	−	+	85, 435, 239, 281, 477 (M-15, not observed)
3-Me C_{33}	34	33.74	+	−	449, 421, 463 (M-15)
C_{34}	34	34.00	+	−	478
13-Me C_{34}	35	34.25	+	−	197, 323, 477 (M-15)
15-Me C_{34}	35	34.25	+	−	225, 295, 477 (M-15)
17-Me C_{34}	35	34.25	+	−	253, 267, 477 (M-15)
11,19-DiMe C_{34}	36	34.51	+	−	183, 351, 309, 225, 491 (M-15)
Z-9-$C_{35:1}$	35	34.72	+	−	490 (173, 411, 584)
Z-7-$C_{35:1}$	35	34.79	+	−	490 (145, 439, 584)
13-Me C_{35}	36	35.30	+	+	197, 337, 491 (M-15)
15-Me C_{35}	36	35.30	+	+	225, 309, 491 (M-15)
17-Me C_{35}	36	35.30	+	+	253, 281, 491 (M-15)
13,17-DiMe C_{35}	37	35.57	+	−	197, 351, 267, 281, 505 (M-15)
15,19-DiMe C_{35}	37	35.57	+	−	225, 323, 253, 295, 505 (M-15)

[a] Carbon number.
[b] Equivalent chain length.
[c] Ion fragments in parentheses are for dimethyldisulphide derivatives of alkenes and alkadienes.
[d] Ion clusters occur as even/odd mass pairs but to save table space only the odd mass fragment of each pair is listed.

branching patterns of 7-, 9-, 10-, and 17-methyl. Dimethyl alkanes (7% of the female hydrocarbons and 17% of the male hydrocarbons) occur as homologous series of 3, 7-, 10, 14-, and 11, 15-dimethyl alkanes, and a series of dimethyl alkanes with branching patterns of 5, 15-, 7, 15-, 12, 16-, and 13, 17-. Unsaturated compounds make up ≈32% of the female hydrocarbons and ≈8% of the male hydrocarbons. The carbon number ranges for the monoenes in the wasps are 29–33, with Z-7- and Z-9- isomers being found. The male wasps possess no dienes, but the females possess small amounts of a conjugated C_{31} diene. Insufficient sample was available to determine double-bond location or stereochemistry of this conjugated diene. No other dienes were found on the females. Five hydrocarbons were shown by analysis of variance (ANOVA) to be significantly different between female and male parasitoids: 11, 15-DiMeC_{29} and 11, 15-DiMeC_{31} are both present in substantially greater proportions in males than in females; Z-9- $C_{31:1}$ and Z-7-$C_{31:1}$ are both present in substantially higher proportions in females than in males, and the conjugated $C_{31:2}$ occurs only in the females (Table 3).

A comparison of the hydrocarbons present on the host ants and the newly emerged parasitoids shows that the wasps and ants share 40 hydrocarbons. For female *Kapala* these 40 compounds represent ≈92.6% of its hydrocarbons. For male *Kapala*, these shared compounds represents ≈84.3% of its hydrocarbons. Finally, these components represent ≈67.7% of the host *Ectatomma* hydrocarbons.

Discussion

An extensive literature exists on social insects and the semiochemical signals that they use to recognize nestmates, conspecifics, and aliens (general reviews: Fletcher and Michener 1987; Hölldobler and Wilson 1990; Howard 1993; Howard and Akre 1995; Vander Meer et al. 1998; studies with ponerine ants: Breed et al. 1990, 1992, 1999; Jeral et al. 1997; Monnin et al. 1998; Tsuji et al. 1999; Liebig et al. 2000). A somewhat smaller literature exists for organisms that invade the nests of social insects and live all or part of their life within the confines of the nest or its immediate environs. Such organisms range in degree of acceptance by the social insects from being completely accepted to those that are almost immediately attacked. The most extensive studies of these interactions involve organisms living with termites (termitophiles) and those living with ants (myrmecophiles). Although a number of explanations have been set forth to explain how these alien organisms gain acceptance from the

Table 2. Percent hydrocarbon composition of *Ectatomma ruidum* workers

Compound	%	Standard deviation
$9,14$-$C_{23:2}$	0.8	0.1
Z-9-$C_{23:1}$	0.9	0.4
C_{23}	0.8	0.1
9-Me C_{23}	0.7	0.5
$9,14$-$C_{25:2}$	1.1	0.8
Z-9-$C_{25:1}$	1.2	0.9
Z-7-$C_{25:1}$	0.6	0.1
C_{25}	1.6	0.4
9-, 11-, 13-Me C_{25}	1.1	0.8
5-Me C_{25}	Tr	—
3-Me C_{25}	0.5	0.4
$5,11$-, $5,13$-DiMe C_{25}	0.3	0.3
C_{26}	1.1	0.4
$3,7$-DiMe C_{25}	Tr	—
10-, 12-Me C_{26}	1.8	0.5
$9,14$-$C_{27:2}$	0.2	0.1
Z-9-$C_{27:1}$	7.4	0.2
Z-7-$C_{27:1}$	2.0	1.0
C_{27}	6.4	2.0
11-, 13-Me C_{27}	9.3	4.2
5-Me C_{27}	1.0	0.7
$11,19$-DiMe C_{27}	0.5	0.2
3-Me C_{27}	2.7	1.0
$5,11$-, $5,13$-DiMe C_{27}	1.0	0.6
C_{28}	1.8	0.7
$3,7$-DiMe C_{27}	Tr	—
10-, 12-Me C_{28}	2.7	0.8
$9,14$-$C_{29:2}$	0.6	0.3
Z-9-$C_{29:1}$	9.2	6.2
3-Me C_{28}	Tr	—
Z-7-$C_{29:1}$	2.8	0.2
C_{29}	5.1	2.8
9-, 11-, 13-Me C_{29}	4.8	1.4
5-Me C_{29}	1.0	0.6
$11,15$-, $13,17$-DiMe C_{29}	Tr	—
$11,19$-DiMe C_{29}	0.8	0.9
3-Me C_{29}	1.7	0.8
$5,9$-DiMe C_{29}	Tr	—
C_{30}	1.1	0.6
$3,7$-DiMe C_{29}	Tr	—
12-Me C_{30}	1.0	0.5
$11,20$-DiMe C_{30} + $C_{31:2}$	0.4	0.3
Z-9-$C_{31:1}$	4.5	0.5
Z-7-$C_{31:1}$	1.3	0.5
C_{31}	1.8	0.4
9-, 11-, 13-, 15-Me C_{31}	2.4	0.6
5-Me C_{31}	0.4	0.3
$11,19$-DiMe C_{31}	1.3	0.7
3-Me C_{31}	0.5	0.4
$5,11$-, $5,13$-DiMe C_{31}	Tr	—
C_{32}	0.6	0.3
$3,7$-DiMe C_{31}	Tr	—
12-Me C_{32}	0.4	0.3
$12,21$-DiMe C_{32}	0.4	0.3
Z-9-$C_{33:1}$	2.7	1.1
Z-7-$C_{33:1}$	0.7	0.4
C_{33}	0.7	0.1
11-, 13-, 15-Me C_{33}	1.4	0.8
$11,21$-, $13,19$-DiMe C_{33}	1.3	0.6
3-Me C_{33}	0.4	0.2
C_{34}	0.2	0.1
13, 15-, 17-Me C_{34}	0.2	0.1
$11,19$-DiMe C_{34}	0.5	0.4
Z-9-$C_{35:1}$	0.9	0.7
Z-7-$C_{35:1}$	0.5	0.2
13-, 15-, 17-Me C_{35}	0.6	0.4
$13,17$-, $15,19$-DiMe C_{35}	0.6	0.3

Means based on two samples of five ants each.

normally pugnacious hosts, the explanation that now seems to have the greatest experimental support is that of chemical mimicry. Under this construct, the inquiline

Table 3. Mean percent hydrocarbon composition of female and male *Kapala sulicifacies*

Compound	Mean percent of total hydrocarbon	
	Female	Male
C_{27}	2.3a	2.4a
9-; 11-; 13-Me C_{27}	3.1a	1.8a
7-Me C_{27}	1.2a	0.3a
5-Me C_{27}	1.1a	0.8a
3-Me C_{27}	2.1a	1.4a
C_{28}	1.2a	1.8a
$3,7$-DiMe C_{27}	0.9a	0.4a
10-; 11-; 12-Me C_{28}	0.9a	1.5a
4-Me C_{28} + $10,14$-DiMe C_{28}	0.4a	0.5a
3-Me C_{28}	0.6a	0.4a
Z-9-$C_{29:1}$	4.7a	1.5a
Z-7-$C_{29:1}$	2.9a	1.0a
C_{29}	10.7a	16.4a
11-; 13-; 15-Me C_{29}	9.4a	14.5a
5-Me C_{29}	2.9a	1.9a
$11,15$-DiMe C_{29}	0.8a	3.0b
3-Me C_{29}	9.3a	9.8a
C_{30} + $3,7$-DiMe C_{29}	1.0a	2.1a
12-Me C_{30}	1.5a	3.4a
4-Me C_{30} + 10, 14-DiMe C_{30}	0.6a	2.2a
Z-9-$C_{31:1}$	17.9a	3.8b
Z-7-$C_{31:1}$	2.7a	0.6b
C_{31}	3.3a	3.2a
$C_{31:2}$ conjugated	0.8a	0.0b
11-; 13-; 15-Me C_{31}	6.4a	6.6a
$11,15$-DiMe C_{31}	2.1a	10.6b
3-Me C_{31}	1.9a	1.4a
C_{32}	0.4a	0.3a
$3,7$-DiMe C_{31}	0.5a	0.4a
12-Me C_{32}	0.5a	0.5a
12, 16-DiMe C_{32}	Tr	Tr
Z-9-$C_{33:1}$	2.2a	0.8a
Z-7-$C_{33:1}$	0.4a	0.6a
C_{33}	0.2a	0.1a
11-; 13-; 15-Me C_{33}	1.1a	1.5a
$11,15$-; 13, 17-DiMe C_{33}	1.7a	0.8a
$7,15$-DiMe C_{33}	1.0a	1.0a
$5,15$-DiMe C_{33}	0.5a	0.4a
13-; 15-; 17-Me C_{35}	0.2a	0.3a

Means based on three samples of five wasps each. All proportional data were arcsine square root transformed and analyzed by one-way ANOVA. Compounds in each row with different letters next to the nontransformed means presented were significantly different at $P = 0.05$ or less.

possesses some chemical signal that mimics chemicals possessed by the host (and which are used by the host as species recognition cues). Although various chemical cues have been postulated, by far the greatest effort has gone into cuticular hydrocarbons. Howard et al. (1980) were the first to postulate that an inquiline (a termitophile) gained total integration into the social life of a colony by having a cuticular hydrocarbon profile that closely mimicked that of its host. They showed that the

Table 4. Comparison of percent composition by class of hydrocarbon between *Kapala sulcifacies* and its host *Ectatomma ruidum*

HC Class	Female *Kapala*	Male *Kapala*	*E. ruidum*
n-alkanes	19.0	26.3	21.2
Branched alkanes	50.3	65.4	41.7
Saturated HC	69.3	91.6	62.9
Unsaturated HC	31.6	8.3	37.2

staphylinid beetle *Trichopsenius frosti* Seevers contained all of the same cuticular hydrocarbons as were found on the host termite, *Reticulitermes flavipes* (Kollar), and that the beetle possessed no other hydrocarbons. They further showed that the beetle biosynthesized all of its cuticular hydrocarbons rather than somehow acquiring them from its host. Subsequent studies showed that another sympatric termite, *R. virginicus* (Banks), had three species of inquilines associated with it, and that all three of these inquilines also showed perfect chemical mimicry of cuticular hydrocarbons with their host (Howard et al. 1982a, 1982b). Furthermore, the hydrocarbon profiles of *R. flavipes* and *R. virginicus* are species-specific, and considerable evidence exists to show that these termites use their cuticular hydrocarbons as species recognition cues (Howard 1993).

Soon after these pioneering studies, Vander Meer and Wojcik (1982) reported on the first instance of chemical mimicry within an ant colony by a scarab beetle that was an inquiline of the imported fire ant, *Solenopsis invicta* Buren. As with the termitophilous beetles, cuticular hydrocarbons were shown to function as semiochemical cues. Unlike the termitophiles, these scarab beetles acquired the hydrocarbons from their host. Once the beetle leaves the ant colony, its own cuticular hydrocarbons once more become predominant.

Not all predacious myrmecophiles use this technique of acquiring hydrocarbons from their host, however. A number of syrphid fly species are obligate larval predators of various ant species, and Howard and his colleagues (Howard et al. 1990a, 1990b) have shown that these fly larvae are much more like the termitophiles than the myrmecophile studied by Vander Meer and Wojcik (1982). The fly larvae were shown to biosynthesize the exact same hydrocarbons as found on the ant hosts and were completely accepted by the ants. Once the adult flies eclosed, however, they were shown to have a number of fly-specific hydrocarbons and to be quickly attacked by the ants if they did not manage to escape the ant nest.

Although many insect orders are known to be inquilines of social insects (Kistner 1979, Hölldobler and Wilson 1990), the parasitic Hymenoptera make up only a small fraction of the known literature and only two prior reports deal with chemical mimicry by these organisms. Jouvenaz et al. (1988) and Vander Meer et al. (1989) report that an *Orasema* sp. (Eucharitidae, Oraseminae), which was later determined as *O. xanthopus* (see Heraty et al. 1993, p. 176), used chemical mimicry to achieve integration in the colonies of its host, the imported fire ant *S. invicta* Buren (Myrmicinae). They examined the pupal and adult stages of the wasp rather than the actively feeding ectoparasitic larvae. The pupae were shown to have cuticular hydrocarbon profiles that are dominated by ant-like patterns, whereas the newly emerged adult wasps possessed hydrocarbon profiles ≈75% identical to that of the ants. Once the adult wasps left the ant nests, the proportion of ant-like cuticular hydrocarbons rapidly diminished to ≈14% (Vander Meer et al. 1989). These authors argued that the wasps procured the hydro-

carbons from their ant hosts rather than biosynthesizing them de novo, but no direct experiments on the issue were conducted.

The life cycle of *K. sulcifacies* (Eucharitidae, Eucharitinae) resembles that of other eucharitid species (Clausen 1941, Heraty et al. 1993, Heraty 1994a). Nevertheless, unlike the Oraseminae where the larva feeds as an ectoparasite on exposed ant larvae, *Kapala* larvae (as all other Eucharitinae larvae) feed on hosts protected by a cocoon and pupate inside the ant cocoon. Accordingly, there is little or no selection pressure for the *Kapala* larvae or pupae to mimic host cuticular hydrocarbons. The newly emerged adult *Kapala*, however, must of necessity interact with the host ants for some period of time before they are able to escape the nest. Ponerines are notoriously aggressive ants, and all are generalist or specialized predators on other arthropods (Wheeler 1910, Dejean et al. 1999). The fact that *E. ruidum* workers do not immediately attack the newly emerged *Kapala* strongly argues for some sort of mimicry or camouflage process. As we have shown, the newly emerged adult wasps share the vast majority of their cuticular hydrocarbons (84.3% for male *K. sulcifacies* and 92.6% for females) with hydrocarbons found on their host ants and this similarity is undoubtedly enough to temporarily inhibit the ant's agonistic behavior. Nevertheless, in spite of this great overlap between wasp and host hydrocarbons, such a similarity does not appear sufficient to suppress completely recognition of parasitoids as colony intruders. This conclusion is suggested both by the number of rejections ouside the nest after transportation by their host which take place almost immediately at emergence, and by the fact that *E. ruidum* workers never feed the adult wasps, even though pseudo-trophallaxis is common between adult workers of this species (Lachaud 1990). Although we have not directly measured the hydrocarbons of these older wasps that are now being attacked, we suspect that like *Orasema*, the *Kapala* cuticular hydrocarbon profile with time begins to differ more and more from the ant profile, eliciting the ants' aggression.

Given that the newly emerged wasps and their host ants seem to share a high proportion of their hydrocarbons, the salient question is mechanistically how does this come about? Do the wasps acquire a large proportion of their hydrocarbons from their hosts, or do they predominately biosynthesize their cuticular hydrocarbons? The *Kapala* larvae could be acquiring at least some host hydrocarbons from the ant larvae or pupae that they have fed upon. Indeed, within such an enclosed environment as the ant-host cocoon, wasp larvae exist in a pool of host odors. Under such a situation, the acquisition of host chemical cues could be attained through a very low cost, passive mechanism. We have recently obtained preliminary data on the hydrocarbon profiles of *E. ruidum* larvae and workers from a single laboratory colony collected at the same site but at a later time (April 2000) from the insects examined above and found that these larvae have essentially the same cuticular hydrocarbons as their adult worker colony mates but in slightly differ-

ent proportions. Because larval and worker ants share essentially the same hydrocarbons then the newly emerged wasp adults could be still carrying over from earlier stages hydrocarbons acquired from feeding or resting on larval hosts. Moreover, if one assumes that older adult hydrocarbon profiles would not appear for a period of a few days, then the presumed acquired ant-like profiles could allow newly emerged adult parasitoids to escape from the host colony, an hypothesis congruent with that proposed by Vander Meer et al. (1989) in the similar association between *O. xanthopus* and *S. invicta.* Such a "flexible" mechanism, easily transposable to different hosts, certainly could account, in part at least, for the very uncommon broad range of potential ant host genera known for the genus *Kapala* (*Pachycondyla, Odontomachus, Ectatomma* and *Gnamptogenys*) (Lachaud et al. 1998b, Lachaud and Pérez-Lachaud 2001).

Unfortunately, unequivocal data supporting such a host-transfer hypothesis for cuticular hydrocarbons is unknown for any insect. In all cases where direct biosynthetic studies have been carried out, the insect biosynthesized de novo essentially all of their cuticular hydrocarbons. No studies have shown significant direct dietary incorporation of host hydrocarbons. Indeed, the only logical way that the newly emerged wasps could possess host- acquired hydrocarbons is by direct mechanical transfer from the cuticle of the host. But because *E. ruidum* larvae and adults have the same hydrocarbons, then if mechanical transfer is occurring one would expect the newly emerged wasps to have on their cuticle essentially all of the ant hydrocarbons and not just some of them as we found. In the absence of direct biosynthesis studies we are unable to establish whether *Kapala* makes its own hydrocarbons or acquires them from its hosts. We are thus left to beg the question of whether all of the hosts parasitized by a species of the genus *Kapala* Cameron do possess very similar hydrocarbons, thus making the development of a biosynthetic mimicry complex somewhat easier, or whether the diet/mechanical hypothesis is the correct one. We would note that in earlier studies with two ant species in the subfamilies Formicinae and Myrmicinae with multiple-host syrphid fly predatory inquiline larvae, the two species of ant larvae had very similar hydrocarbon profiles (dominated by n-alkanes), whereas the corresponding adult ants had very disparate and species-specific profiles (Howard et al. 1990a, 1990b; Howard and Akre 1995). In those cases, the mimicry complex was with the ant larvae and not with the adult ants. Further experimentation will be required to clarify the mimicry status of wasps in the genus *Kapala* associated with its various host ponerine ants.

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